The diet of sperm whales (*Physeter macrocephalus*) in southern Australian waters

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Stomach contents were collected from 36 sperm whales (*Physeter macrocephalus*) involved in two mass stranding events during February 1998 along the west coastline of Tasmania, Australia. Contents were dominated by oceanic cephalopods, with a total of 101 883 cephalopod beaks representing 48 species from 14 families of Teuthids, two species from two families of Octopods, and a single Vampyromorph species identified. Species diversity was higher in these animals than other sperm whales studied in the southern hemisphere, with samples containing an average of ($\pm$ s.d.) 28.4 $\pm$ 11.1 species per sample. Diet samples were dominated by subtropical and muscular cephalopod species. Members of the family Histioteuthidae were the most important numerically, and were also important in terms of estimated reconstituted mass, although members of the Onychoteuthidae were the most dominant species in samples in terms of estimated reconstituted mass. Other families numerically important to species composition included the cranchiid, lepidoteuthid, onychoteuthid, and pholidoteuthid families, while the architeuthid, pholidoteuthid, and ommastrephid families were also important in terms of reconstituted mass. Cephalopod species composition varied with stranding site and with sex, but not with age. However, differences did not represent systemic variation with groups marked by high individual variability. Lower rostral lengths of all cephalopod species ranged from 1.3 to 40.7 mm. Calculated dorsal mantle lengths from all species ranged from 10.7 to 2640.7 mm (mean $\pm$ s.d. = 233.7 $\pm$ 215.7 mm) and estimated wet weights of cephalopod prey ranged from 2.7 to 110 233.1 g (mean $\pm$ s.d. = 828.3 $\pm$ 3073.6 g). While there were differences in the size of some cephalopod species between stranding sites and with age, this was marked by high individual variability. Differences in diet composition and prey size between sperm whales reflect individual variability in foraging success and perhaps also foraging groups related to the social structure of this species.

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Introduction

With the management of recovering whale populations a high priority for national and international environmental managers (Taylor and Dizon, 1999), and the need to derive better understanding of energy flow and trophic links in marine systems due to increasing fisheries pressure and global warming (Brodie and Påsche, 1982; Simmonds and Mayer, 1997), a more comprehensive understanding of the diet of marine predators, particularly large top-order predators, is needed. In order to quantify natural variations in the foraging relationships of predators within an ecosystem, these assessments must be conducted over appropriate temporal scales and for wide-ranging and migratory species, assessments must also cover appropriate spatial scales. However, attaining quantitative assessments of the diet of pelagic, wide-ranging, deep-diving predators such as sperm whales (*Physeter macrocephalus*) is difficult.

Cephalopods are a key trophic link in the Southern Ocean ecosystem and form an important part of the diet of many marine animals including whales, seals, birds, and fish (Clarke, 1983). It has been estimated that in the

Southern Ocean alone, some 34 million tonnes of cephalopods are consumed by vertebrate predators annually and nearly 12 million tonnes of this specifically by sperm whales (Clarke, 1983; Rodhouse, 1989). Dietary information for sperm whales has been derived from stomach contents collected from a small number of beach-stranded and numerous whaling industry animals throughout the southern hemisphere (Gaskin and Cawthorn, 1967; Clarke et al., 1976; Clarke, 1980; Clarke and MacLeod, 1982; Pascoe et al., 1990; Clarke and Roeleveld, 1998). However, such information on this species in the Southern Ocean is still sparse.

Data derived from whaling operations are often biased towards adult animals, particularly males, and disregard any dietary assessments on smaller spatial scales, especially in terms of individual pods or groups. Diet studies other than those derived from whaling are largely based on small numbers of stranded animals or on small numbers of faecal samples from spatially separated individuals (e.g. Santos et al., 1999; Smith and Whitehead, 2000). For a large proportion of stranded animals, particularly those involved in single strandings, cause of death is unknown and is often possibly associated with disease. Consequently, dietary assessments from such individuals may not reflect that of the healthy population. Mass-stranded animals, however, are thought to be largely free of biases associated with disease (Aguilar et al., 1999). Faecal studies are limited as they can only ever report on partial samples. This is due to the identification of prey being restricted to hard part remains and of those, larger hard parts may sink before collection is possible, smaller parts may pass through meshed collecting devices and sampling is likely not to encompass all of the faeces passed by the animal. Differential digestion of species may further bias the results of faecal studies to particular species (Smith, 1992).

An assessment of diet on a much smaller scale than before was made possible through the mass stranding of three groups of sperm whales on the west and north coasts of Tasmania in February 1998 (Evans et al., 2002). Stomach samples from these animals provided a unique opportunity to compare diet of individuals between and among sperm whale groups and also across a range of age classes.

Methods

Contents were collected from the stomachs of 36 sperm whales involved in two mass strandings (STR1: Ocean Beach, Strahan: n = 15; STR2: Greens Pt. Beach, Marrawah: n = 21; Table 1). These were part of a series of three mass strandings of this species that occurred on the west and north coasts of Tasmania in 1998 (Evans et al., 2002; Figure 1).

Samples were collected from whales post mortem 48 h after the stranding was reported at STR1 and 24 h after reporting at STR2. Full contents were often not collected

Table 1. Total dorsal length and age of sperm whales sampled from two mass strandings (excluding foetuses), Tasmania, Australia.

		All stranded sperm whales			Diet subsample		
		All	Female	Male	All	Female	Male
STR1	Dorsal total length (cm) Mean ± s.d.	1045.8 ± 144.2	1051.9 ± 136.9	667.0	1054.5 ± 105.4	1054.5 ± 105.4	—
	Range (n)	417.0–1200.0 (63)	417.0–1200.0 (62)	667.0 (1)	720.0–1144.0 (14)	720.0–1144.0 (14)	—
	Age (No. GLGs*) Mean ± s.d.	31.5 ± 11.8	32.0 ± 11.2	1.9	32.2 ± 13.1	32.2 ± 13.1	—
	Range (n)	0.75–53.0 (56)	0.75–53.0 (55)	1.9 (1)	7.0–53.0 (12)	7.0–53.0 (12)	—
STR2	Dorsal total length (cm) Mean ± s.d.	1069.4 ± 42.4	1043.6 ± 104.6	1055.5 ± 107.7	1045.7 ± 74.3	1058.7 ± 42.4	1013.3 ± 123.6
	Range (n)	575.0–1150.0 (35)	575.0–1130.0 (25)	780.0–1150.0 (10)	780.0–1120.0 (21)	980.0–1120.0 (15)	780.0–1120.0 (6)
	Age (No. GLGs*) Mean ± s.d.	33.5 ± 15.3	38.1 ± 14.4	19.3 ± 6.6	31.7 ± 13.5	37.7 ± 11.3	18.7 ± 6.9
	Range (n)	1.5–64.0 (29)	1.5–64.0 (22)	5.0–24.0 (7)	5.0–58.0 (19)	24.0–58.0 (13)	5.0–24.0 (6)

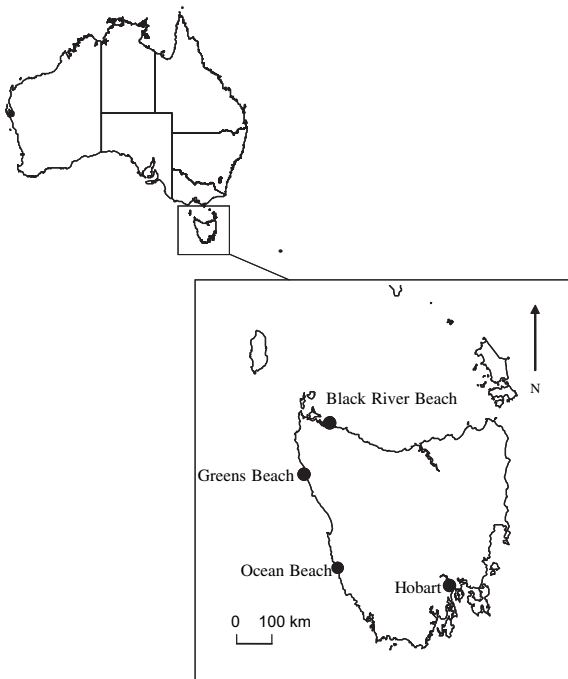*Not all animals measured for dorsal total length were aged.

Figure 1. Location of sperm whale strandings, Tasmania, Australia 1998.

due to an inability to access the whole stomach and time constraints, but in most cases, the complete contents of the second stomach (the primary area in which food remains are found) were collected. In all cases the relative proportion of contents collected was estimated. Complete stomach contents were collected from 47% of animals (sampling group A), contents were collected from the second stomach only in 50% of all animals (sampling group B), and contents were collected from only part of the second stomach in 3% of all animals (sampling group C). Contents were frozen at −20°C on return to the University of Tasmania.

Sample analyses

Stomach samples were thawed, washed, and sieved with a 0.5 mm sieve and then sorted into major taxonomic classes. Hard part remains were separated from soft parts and identified to the lowest taxon possible. In most cases this was to genus, but the state of digestion sometimes restricted this to order or class. Identification of teleost and elasmobranch hard parts was carried out using the reference collections of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Marine Research laboratories, Hobart. Cephalopod beaks were separated from other cephalopod hard part remains and sorted into upper and lower beaks. The lower beaks were identified to the lowest taxonomic level possible using Voss (1969), Clarke (1986), and a voucher collection of cephalopod beaks

housed at the Australian Antarctic Division, Hobart. All cephalopod identifications were additionally verified against the cephalopod collections at the Museum of Victoria, Melbourne. Among those beaks within the family Histioteuthidae that could not be resolved to the species level, beaks were separated into those of Types A and B (as per Clarke, 1986) and where possible classified into species groups as described by Clarke (1980, 1986). Cephalopod species were subsequently classified where possible in terms of their distribution (ecotype), tissue composition, and vertical distribution using relevant literature on the biology, physiology, and ecology of cephalopods (see Table 3 for a complete listing of references used). Ecotypes were defined as tropical (occurring around equatorial regions 0°−20°S), subtropical (known to occur north of the subtropical convergence at approximately 40°S, but south of equatorial regions), sub-Antarctic (known to occur south of the subtropical convergence), or Antarctic (known to occur south of the Antarctic Polar Front at approximately 55°S). Where species spanned a number of ecotype regions (e.g. tropical/subtropical), the ecotype region at the centre of their distribution was used. Note that our classification of tissue composition differs to that of M. R. Clarke's division of gelatinous (neutrally buoyant) and muscular (negatively buoyant) species [see Clarke (1966, 1980, 1986)]. However, there is some flexibility in this definition with families such as the gonatids, which are neutrally buoyant through the use of oil contained in the liver, being classified muscular due to the high calorific content of this oil (Clarke *et al.*, 1985). In an effort to provide an objective assessment of tissue composition, our division was based on the identification of the presence of muscular tissue within a species or family.

Lower rostral lengths (LRLs) for squid and lower hood lengths (LHLs) for octopods were measured with vernier callipers to the nearest 0.1 mm. Allometric regression equations were used to estimate dorsal mantle length (DML) and wet body mass of individual cephalopods and octopods from LRLs and LHLs (Wolff, 1984; Clarke, 1986; Rodhouse *et al.*, 1990; Lu and Williams, 1994; Jackson *et al.*, 1997; Lu and Ickeringill, 2002). While many of these equations are based on too few specimens and therefore may not be accurate for some size classes, they provide a general guide to the size and weight of prey items (Clarke and Young, 1998). Due to these limitations, all comparative analyses of prey size were conducted on LRLs or LHLs rather than on estimated DML or wet body mass.

Statistical analyses

Given the importance of cephalopods in the diet of this species elsewhere, and the predominance of cephalopods in the samples examined here, statistical analyses focused only on this prey group. Each individual whale was assigned an age based on counts of the number of growth layers in a tooth taken from that animal (Evans and

Robertson, 2001; Evans *et al.*, 2002; Table 1) and then assigned to age groups based on approximate maturity of individuals (Lockyer, 1981; Rice, 1989). These corresponded to: (1) juvenile or immature (female: ≤ 13 yr; male: ≤ 18 yr); (2) sexually mature but not physically mature (female: $> 13 \leq 30$ yr; male: $> 18 \leq 35$ yr); and (3) sexually and physically mature (female: > 30 yr; male: > 35 yr).

Because the relative proportion of stomach contents collected differed across samples, it was important to establish whether these differing proportions biased the species diversity of each sample observed. Data were log-transformed and an analysis of covariance (ANCOVA) was used to determine if there was any interaction between the sampling group and the total number of beaks and whether the sampling group influenced the relationship between the number of species groups and the total number of beaks. As group C contained only one sample, only those data from groups A and B were tested.

Patterns in the cephalopod species composition data (percentage numerical abundance expressed as a percentage of the total number of beaks) were visualized via ordination using non-metric multidimensional scaling (MDS) based on a Bray-Curtis similarity matrix. Data were log $+ 1$ transformed prior to analyses. A one-way analysis of similarity (ANOSIM) over 99 random starts was then used to ascertain whether the diet of individuals differed on the basis of site, sex, and age. Similarity percentages (SIMPER) were determined in order to ascertain those cephalopod species responsible for any statistically significant differences observed between groups with ANOSIM.

The percentage numerical abundance and abundance by percentage weight of cephalopod species from each ecotype and composition group in samples were compared between stranding sites, sex, and age groups. Data were arcsine transformed and tested via a one-way nested ANOVA. Because of small sample sizes, immature animals were excluded from the data set.

The mean LRLs of each cephalopod species contained in samples were compared between stranding sites and age groups using a one-way nested ANOVA. Data were tested for homogeneity and log-transformed if heterogeneous before conducting the nested ANOVA. Because of small sample sizes, immature animals and males were excluded from the data set.

Results

Stomach contents were dominated by intestinal nematodes and cephalopod beaks (Table 2), both of which occurred in all stomachs. While fragments of flesh occurred in 97% of all samples, these were in varying stages of decomposition and at least some consisted of partially decomposed gastro-intestinal lining.

Non-cephalopod component of the diet

Non-cephalopod remains in the stomachs of sperm whales were dominated by intestinal nematodes, which were present in all samples and represented almost all of the undigested material present in each sample. Small numbers of fish bones and otoliths, crustacean exoskeletons, a gastropod, and plastic debris were also present (Table 2). Identifiable fish remains were sparse, occurring in 16.7% of all samples, and were limited to hard parts. Two samples contained one highly eroded otolith each from the family Myctophidae, one sample contained a number of partially digested cartilaginous parts from an unidentified elasmobranch and a vertebral section from an unidentified teleost. Four samples contained single vertebral segments from unidentified teleosts. Small sections of unidentifiable crustacean exoskeletons were present in 44.4% of samples and one sample (2.8% of all samples) contained one unidentified gastropod. Small pieces of plastic material were present in four samples (11.1% of all samples), one of which also contained the top section of a plastic container (of approximately 2 l in reconstructed volume). Three animals (0.75, 1.5, and 7 yr) had what appeared to be a milk-like substance present in their stomachs. Only the oldest of the three had hard part remains in the form of cephalopod beaks also present.

Cephalopod component of the diet

Cephalopod remains included beaks, partial gladii, complete and partial eye lenses, and sucker rings and hooks. No buccal masses were identified in any of the samples. Remains of cephalopod gladii were found in 66.7% of all samples, whole or part cephalopod eye lenses were found in 94.4%, and cephalopod sucker rings and hooks were found in 11.1%. Cephalopod beaks were present in all samples. A total of 101 883 cephalopod beaks (52 109 upper beaks, 49 774 lower beaks) were recovered from the 36 animals, representing species from three cephalopod orders, Teuthida, Octopoda, and Vampyromorphida. Teuthids were represented by 48 species from 14 families, octopods by two species from two families and the Vampyromorphida by the one species *Vampyroteuthis infernalis* (Table 3). The average number of species present across all samples was 28.4 ± 11.1 per samples (range: 4−45).

The proportion of stomach contents sampled did not appear to have an effect on the species diversity of samples. No significant interaction was observed between the sampling group and the total number of beaks ($F = 1.4$, d.f. $= 1$, $p = 0.2$), nor did the sampling group appear to have a significant effect on the relationship between the number of species groups and the total number of beaks ($F < 0.001$, d.f. $= 1$, $p = 0.9$). Subsequent analyses were therefore not restricted to those samples within individual sampling groups.

Table 2. Composition of stomach content remains by frequency of occurrence (%) in sperm whales from southern Australian waters.

Dietary group	n	Cephalopods	Fish	Nematodes	Invertebrates	Plastics	Unidentified flesh	Unidentified
All	36	100.0	16.7	100.0	44.4	11.1	97.2	2.8
STR1	15	100.0	6.7	100.0	53.3	13.3	100.0	0.0
STR2	21	100.0	23.8	100.0	38.1	9.5	95.2	0.0
Immature	2	100.0	0.0	100.0	33.3	0.0	100.0	0.0
Sexually mature	14	100.0	28.6	100.0	42.9	7.1	92.9	0.0
Physically mature	15	100.0	13.3	100.0	46.7	20.0	100.0	6.7
All Female	30	100.0	10.0	100.0	46.7	13.3	96.7	3.3
Immature F	1	100.0	0.0	100.0	0.0	0.0	100.0	0.0
Sexually mature F	9	100.0	11.1	100.0	55.6	11.1	88.9	0.0
Physically mature F	15	100.0	13.3	100.0	46.7	20.0	100.0	6.7
All Male	6	100.0	50.0	100.0	33.3	0.0	100.0	0.0
Immature M	1	100.0	0.0	100.0	100.0	0.0	100.0	0.0
Sexually mature M	5	100.0	60.0	100.0	20.0	0.0	100.0	0.0

Cephalopod species composition

Members of the histioteuthid family dominated samples by number and by frequency of occurrence. The species *Histioteuthis* B4 was the most numerous (7127 lower beaks, 14.2% numerical abundance; Table 3). Other important species both numerically and by frequency of occurrence included *Histioteuthis* B2 (6202, 12.5%N), *Histioteuthis atlantica* (4739, 9.5%N), *Lepidoteuthis grimaldii* (4632, 9.3%N), and *Histioteuthis bonnellii* (2782, 5.6%N). Of the total 51 species, 25 accounted for over 92% of numerical abundance.

Estimated fresh wet mass for all species identified were not available due to a lack of regression equations for three species (*Discoteuthis discus*, *Japatella* sp., and *L. grimaldii*). This not only prevents the interpretation of the contribution of these species to overall mass, it also limits the interpretation of the contribution of other species to overall mass. Of those species for which fresh wet mass was calculated, the histioteuthids collectively were also important by weight, contributing 14.3% to the total estimated mass, with the family Onychoteuthidae contributing the largest proportion by weight (36.5%; Table 3). Of the total of 48 species for which regressions were available, 13 accounted for over 90% of the estimated total wet weight. *Moroteuthis robsoni* (32.5%), *Architeuthis* sp. (13.6%), *Pholidoteuthis boschmai* (11.4%), *Todarodes filippovae* (6.6%), and *Taningia danae* (5.0%) were important species in terms of total estimated wet mass.

Cephalopod species composition with respect to stranding group, sex, and age

Multidimensional scaling of species composition data produced the groupings illustrated in Figure 2. The best 2-D configuration associated with MDS produced a stress of 0.11 and the best 3-D configuration produced a stress of 0.08. The results of the ANOSIM reflected the ordination produced by the MDS. Cephalopod species composition differed significantly between sexes (Global R: 0.307,

significance level: 0.036), but not age groups (Global R: 0.065, significance level: 0.21). Differences between stranding sites were statistically non-significant, but it is likely that these differences are biologically significant (Global R: 0.093, significance level: 0.069). The similarity/ dissimilarity breakdowns produced by SIMPER identified the abundances of *P. boschmai*, *H. bonnellii*, *M. robsoni*, *Mesonychoteuthis hamiltoni*, *Histioteuthis* B2, and *H. atlantica* as those contributing to the differences observed between the two stranding sites (Table 4). The abundances of *M. hamiltoni*, *M. robsoni*, *H. bonnellii*, *Histioteuthis* B2, and *Galiteuthis glacialis* were most important in contributing to the differences observed between sexes (Table 4).

Overall, diet samples were dominated by subtropical and muscular species (Table 2; Figures 3 and 4). The numerical abundance of species in each ecotype group was significantly different between stranding groups ($F_{1,3} = 10.7$, $p = 0.04$), sexes ($F_{1,3} = 46.9$, $p = 0.01$), and age groups ($F_{1,3} = 617.6$, $p < 0.001$). Individuals from STR1 contained higher abundances of subtropical species, while those from STR2 contained higher abundances of sub-Antarctic and Antarctic species. Females contained higher abundances of tropical and subtropical species, while males contained higher abundances of Antarctic species. Immature animals contained higher abundances of subtropical and Antarctic species. Comparisons between the abundance of species in each ecotype on the basis of percentage weight reflected that of numerical abundances with statistically significant differences observed between stranding groups ($F_{1,3} = 8.8$, $p = 0.05$), sexes ($F_{1,3} = 15.6$, $p = 0.02$), and age groups ($F_{1,3} = 315.7$, $p < 0.001$). The abundance of muscular and gelatinous cephalopod species was not significantly different between stranding sites, sexes, or age groups both in terms of numerical abundance (site: $F_{1,1} = 0.001$, $p = 0.9$; sex: $F_{1,1} = 0.01$, $p = 0.9$; age: $F_{1,1} = 0.3$, $p = 0.6$) or percentage weight abundance (site: $F_{1,1} = 0.1$, $p = 0.7$; sex: $F_{1,1} = 0.04$, $p = 0.8$; age: $F_{1,1} = 0.1$, $p = 0.7$).

Table 3. Distribution, composition, maximum recorded size, frequency of occurrence (FOO), abundance by number (expressed as a percentage of the total number of beaks, %N), and percentage of total mass (%W) of cephalopod species identified from the stomachs of sperm whales from Tasmania (all samples pooled, n = 36).

Species	Ecotype	Tissue composition	Depth distribution (m)	Maximum GL/ML/TL (mm)	FOO	%N	%W
Haliphron atlanticus	sa	g	0−3 180	108ML	11.1	0.03	0.04
Allopsidae					11.1	0.03	0.04
Ancistrocheirus lesueuri	st	g	80−2 000	390ML	69.4	2.1	3.8
Ancistrocheiridae					69.4	2.1	3.8
Architeuthis sp.	st	m	295−1 100	4 000ML	72.2	1.0	13.6
Architeuthidae					72.2	1.0	13.6
Japetella sp.	t	g	0−4 000	>20ML	25.0	0.1	n/a
Bolitaneidae					25.0	0.1	n/a
Chiroteuthis joubini	st	g	n/a	155ML	63.9	0.7	0.2
Chiroteuthis veryani	sa	g	250−2 000	91ML	88.9	2.8	0.6
Chiroteuthis sp.	n/a	g	200	107ML	22.2	0.1	0.01
Chiroteuthidae					91.7	3.5	0.8
Chtenopteryx sp.?	st	m	0−2 000	83ML	2.8	0.002	0.0001
Chtenopterygidae					2.8	0.002	0.0001
Cranchia scabra	t	g	190−3 500	130ML	36.1	0.1	0.01
Galiteuthis glacialis	a	m	0−1 000	496ML	91.7	2.7	0.3
Galiteuthis pacifica	t	m	500−800	65GL	8.3	0.01	0.001
Megalochranchia sp.	st	g	0−400	880ML	55.6	1.2	0.2
Mesonychoteuthis hamiltoni	a	g	0−2 560	4000TL	86.1	1.6	2.1
Taonius pavo	st	g	0−1 000	539ML	77.8	2.0	0.7
Teuthowenia pellucida	st	m	0−2 400	200ML	80.6	1.8	0.6
Cranchiidae					100.0	9.4	3.9
Cycloteuthis akimushkini	st	m	0−650	480ML	2.8	0.002	0.004
Discoteuthis discus	st	m	0−950	155ML	11.1	0.03	n/a
Cycloteuthidae					13.9	0.03	0.004
Gonatus antarcticus	a	m	0−2 100	345ML	47.2	0.1	0.1
Gonatidae					47.2	0.1	0.1
Histioteuthis A1	n/a	n/a	n/a	n/a	5.6	0.1	0.04
Histioteuthis macrohista	sa	m	200−2 500	67ML	55.6	0.6	0.1
Histioteuthis melaegroteuthis	st	m	100−1 875	114ML	52.8	0.6	0.1
Histioteuthis bonnellii	st	m	70−2 000	330ML	69.4	5.6	1.5
Histioteuthis celetaria pacifica	t	m	200−1 200	234ML	22.2	0.03	0.01
Histioteuthis miranda	st	m	0−3 000	300ML	63.9	1.1	0.9
Histioteuthis hoylei	st	m	100−800	210ML	55.6	2.1	0.9
Histioteuthis sp. Type A	n/a	n/a	n/a	n/a	25.0	0.2	0.1
Histioteuthis B1	st	n/a	n/a	n/a	63.9	2.5	0.7
Histioteuthis eltaninae	sa	g	30−2 890	105ML	63.9	3.6	0.7
Histioteuthis B2	st	n/a	n/a	n/a	94.4	12.5	3.0
Histioteuthis reversa	st	m	60−1 800	186ML	27.8	0.8	0.1
Histioteuthis atlantica	st	m	0−2 500	258ML	91.7	9.5	2.3
Histioteuthis B4	st	m	n/a	n/a	100.0	14.3	3.6
Histioteuthis sp. Type B	n/a	n/a	n/a	n/a	77.8	1.0	0.3
Histioteuthidae					100.0	54.7	14.3
Lepidoteuthis grimaldii	st	m	0−700	970ML	97.2	9.3	n/a
Lepidoteuthidae					97.2	9.3	n/a
Idioteuthis cordiformis	st	m	n/a	87ML	75.0	0.9	0.4
Mastigoteuthis psychrophile	a	m	400−1 200	n/a	5.6	0.01	0.0002
Mastigoteuthis sp.	n/a	n/a	n/a	n/a	27.8	0.1	0.01
Mastigoteuthidae					75.0	1.0	0.4
Octopoteuthis rugosa	st	m	?−1 500	230ML	80.6	2.0	0.7
Taningia danae	st	m	0−900	>1 400ML	72.2	0.6	5.0
Octopoteuthidae					88.9	2.7	5.6
Nototodarus gouldi	st	m	100−1 130	412ML	72.2	0.7	2.6

(*continued*)

Table 3 (*continued*)

Species	Ecotype	Tissue composition	Depth distribution (m)	Maximum GL/ML/TL (mm)	FOO	%N	%W
Ommastrephes bartrami	st	m	0−2 000	800ML	41.7	0.1	0.4
Todarodes filippovae	sa	m	35−2 000	530ML	88.9	2.2	6.6
Ommastrephidae					91.7	3.9	9.6
Kondakovia longimana	a	m	0−860	940ML	86.1	1.3	2.7
Moroteuthis 'A'/ingens	sa	m	25−1 025	>520ML	66.7	0.3	0.7
Moroteuthis knipovitchi	a	m	0−550	450ML	63.9	0.7	0.3
Moroteuthis lonnbergii	st	m	100−920	275ML	63.9	0.4	0.4
Moroteuthis robsoni	st	m	40−260	900ML	91.7	2.7	32.5
Onychoteuthidae					94.4	5.3	36.5
Pholidoteuthis adami	st	m	360−925	31ML	13.9	0.03	0.01
Pholidoteuthis boschmai	sa	m	0−2 000	580ML	91.7	4.6	11.4
Pholidoteuthidae					91.7	4.7	11.4
Vampyroteuthis infernalis	st	g	500−4 850	100ML	27.8	0.04	0.03
Vampyroteuthidae					27.8	0.04	0.03
Unidentified					72.2	2.1	n/a

Ecotypes: t: tropical; st: subtropical; sa: sub-Antarctic; a: Antarctic. Tissue composition: m: muscular; g: gelatinous. Length: GL: gladius length; ML: maximum dorsal length recorded in mm; TL: maximum total length recorded in mm; n/a: not available. Details of cephalopods derived from: Clarke, 1966, 1980, 1986; Voss, 1969, 1985; McSweeny, 1970, 1976; Nesis, 1972, 1987; Roper and Young, 1975; Imber, 1978; Korzun *et al.*, 1979; Roper *et al.*, 1984; Dunning, 1985, 1988, 1993, 1998; Dunning and Brandt, 1985; Hatanaka *et al.*, 1985; Nemoto *et al.*, 1985; Rodhouse and Clarke, 1985; Robison, 1989; Rodhouse *et al.*, 1992; Lipiński, 1993; Alexeyev, 1994; Lu and Williams, 1994; Piatkowski and Hagen, 1994; Rodhouse and Piatkowski, 1995; Lordan *et al.*, 1998; Rodhouse and Lu, 1998; Jackson *et al.*, 2000; Collins *et al.*, 2001; CIAC Beak Database, Version 1.0, 2001; GIS of squid distribution in the Southern Ocean, 2001 (http://www.nerc-bas.ac.uk/public/mlsd/squid-atlas/); The Tree of Life Web Project, 2001 (http://www.tolweb.org/tree/); Cephbase, 2002 (http://www.cephbase.utmb.edu/).

Size of cephalopods
The size of cephalopod prey varied considerably. Lower rostral lengths of all species ranged from 1.3 to 40.7 mm (Table 5) and calculated DMLs from all species ranged from 10.7 to 2640.7 mm with a mean size of prey consumed of 233.7 ± 215.7 mm (Table 5). Only *Architeuthis* sp., *L. grimaldii*, *M. hamiltoni*, *M. robsoni*, and *T. danae* were represented by individuals calculated to have had DMLs larger than 1000 mm. Cephalopods larger than 1000 mm comprised only 0.6% numerically of all cephalopods present in the samples, while those less than 300 mm comprised 73.5% (Figure 5). Estimated wet masses also varied considerably, ranging from 2.7 to 110 233.1 g (Table 5) with a mean estimated wet mass of 828.3 ± 3073.6 g. Twenty species were represented by individuals greater than 1000 g estimated wet mass and those larger than 1000 g comprised 78.6% of the estimated total wet mass (Figure 6).

Size of cephalopods with respect to stranding and age groups
Mean LRLs of 20 cephalopod species present in samples differed significantly between stranding sites, and mean LRLs of 17 species differed significantly between the age groups 2 and 3 (Table 6). Individuals from STR1 contained larger beaks of *Architeuthis* sp., *L. grimaldii*, *Moroteuthis lonnbergii*, the ommastrephids, and *Octopoteuthis rugosa*

while those from STR2 contained larger beaks of *Chiroteuthis veryani*, the Type A histioteuthids, *Idioteuthis cordiformis*, *M. hamiltoni*, *M. robsoni*, and *Taonius pavo*. Individuals from age group 2 contained larger beaks of *G. glacialis*, most histioteuthids, and *Kondakovia longimana*, while those from age group 3 contained larger beaks of the *Cranchia scabra*, *Teuthowenia pellucida*, *Histioteuthis macrohista*, *Histioteuthis* B1, *L. grimaldii*, and the three *Moroteuthis* species (Table 6).

Discussion

The results from this study suggest that southern Australian sperm whales predominantly feed on oceanic cephalopods. The diet of these sperm whales demonstrates a high degree of individual variability, suggesting individuals opportunistically consume those species present and most abundant in the area of foraging. Our current knowledge of the diet and foraging behaviour of this species suggest that sperm whales have evolved to become highly voracious specialized predators on an extremely abundant prey source.

Samples obtained from stranded animals may be subject to a number of biases, such as differential digestion of prey items, retention of hard part remains, lack of representation of temporal variability in prey items, and inability to discern primary from secondarily digested prey. As a result, the importance of particular prey items may not reflect that
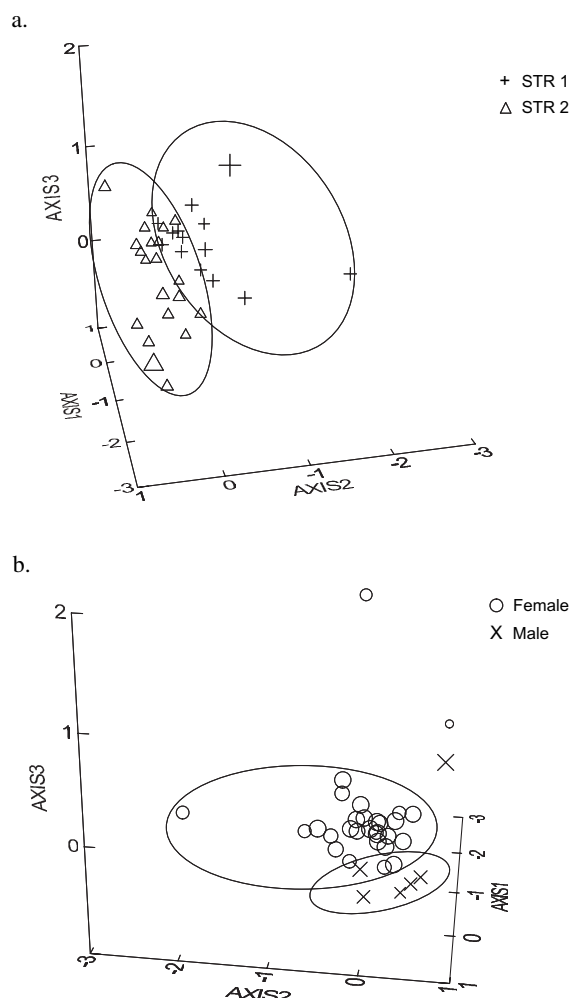
Figure 2. Three-dimensional plot of the results of multidimensional scaling conducted on the cephalopod species composition of samples (a) between STR1 and STR2 and (b) between males and females.

a result, stranding events provide a unique window of opportunity into a component of the foraging ecology of sperm whales.

Non-cephalopod component of the diet

Digestion of the soft parts of cephalopods is rapid in sperm whales (Clarke, 1980) and that of muscular cephalopod species is more rapid than digestion of teleosts (A. J. Read, pers. comm.). Therefore, the lack of fish remains and the presence of cephalopod gladii, eyes, sucker rings and hooks in the stomachs of these animals suggests that fish did not play an important role in the diet of the sperm whales involved in these strandings in the few days prior to the stranding events. In a number of sperm whale diet studies, fish have been observed to be regular but minor contributors to the overall diet of this species (Clarke, 1980; Kawakami, 1980; Santos *et al.*, 1999; see Roe, 1969; Martin and Clarke, 1986 for exceptions to this). Fish remains were found in 50% of males in this study in comparison to only 10% of females, and may be indicative of differences in foraging habitats between sexes as suggested in other studies (Clarke *et al.*, 1988). However, the number of males in this study was small and may not be representative of the larger population.

Crustaceans have also been reported in the diet of sperm whales throughout the southern hemisphere and include mysids and crabs (Clarke, 1980; Clarke *et al.*, 1988; Rice, 1989). It is not clear whether these are (i) ingested incidentally during normal feeding, (ii) are targeted as specific prey, or (iii) are secondarily ingested via the stomachs of fish or squid prey. Intestinal nematodes are commonly found in large numbers in the stomachs of sperm whales (Rice, 1989). If it is assumed that the wet weight of nematodes and the estimated total wet weight of cephalopods in each sample is largely representative of the total wet weight of each stomach sample, nematodes in the stomach of the sperm whales in this study comprise $0.3 \pm 0.9\%$ (range: 0.01–5.7%) of the total wet weight of stomach contents.

Cephalopod component of the diet

Cephalopod species composition

The number of cephalopod species observed in the stomachs of sperm whales in this study is higher than that recorded elsewhere (Gaskin and Cawthorn, 1967; Clarke and MacLeod, 1974; Clarke and MacLeod, 1976; Clarke *et al.*, 1976; Clarke, 1980; Clarke and MacLeod, 1982; Fiscus *et al.*, 1989; Pascoe *et al.*, 1990; Smith, 1992; González *et al.*, 1994; Clarke and Roeleveld, 1998; Clarke and Roper, 1998; Clarke and Young, 1998; Smith and Whitehead, 2000) and encompasses tropical to Antarctic, muscular and gelatinous, pelagic, mesopelagic, bathypelagic, and mesobathypelagic species. The lower species diversity documented in other studies may be reflective of

of the true diet of the individual. However, obtaining an unbiased assessment of the diet of this species is difficult. Novel techniques such as the analysis of faecal DNA (Jarman *et al.*, 2002) in association with investigations into hard part remains may provide a more comprehensive insight into the diet of top predators. Fatty acid signature analysis on blubber derived from live animals via the use of biopsies may provide greater insight into temporal variation in the diet of sperm whales. However, due to a lack of knowledge on the occurrence and distribution of sperm whales in the Australian region, the viability of faecal sampling or biopsy programmes involving live animals has not yet been established. Fatty acid signature analysis is additionally presently limited to coarse scale diet structure and is yet to be proven to be successful at discriminating fine scale diet composition (Bradshaw *et al.*, 2003). As

Table 4. Percentage abundance of cephalopod species identified by similarity percentages (SIMPER) contributing to cephalopod species composition differences between sperm whales from STR1 and STR2 and between female and male sperm whales (cut off for low contributions: 50%).

	Site				Sex				
Species	Mean abundance (STR1)	Mean abundance (STR2)	Mean dissimilarity ± s.d.	Cumulative contributing %	Species	Mean abundance (female)	Mean abundance (male)	Mean dissimilarity ± s.d.	Cumulative contributing %
P. boschmai	2.7	8.5	2.0 ± 1.1	4.8	*M. hamiltoni*	1.7	10.7	2.7 ± 1.4	6.3
H. bonnellii	3.5	4.7	2.0 ± 1.3	9.6	*M. robsoni*	2.8	12.6	2.5 ± 1.6	12.1
M. robsoni	1.7	6.3	1.9 ± 1.3	14.2	*H. bonnellii*	4.6	2.5	2.1 ± 1.4	17.0
M. hamiltoni	0.8	4.8	1.8 ± 1.1	18.5	*Histioteuthis* B2	12.9	4.6	1.9 ± 1.5	21.3
Histioteuthis B2	15.2	9.0	1.7 ± 1.0	22.7	*G. glacialis*	5.0	1.2	1.8 ± 1.0	25.6
H. atlantica	9.3	9.6	1.6 ± 0.9	26.7	*P. boschmai*	5.8	7.9	1.8 ± 1.2	29.8
G. glacialis	2.1	5.9	1.6 ± 0.9	30.7	*H. eltaninae*	3.1	0.4	1.7 ± 1.4	33.7
H. eltaninae	2.3	2.9	1.6 ± 1.3	34.6	*H. atlantica*	9.2	10.5	1.5 ± 1.0	37.3
T. filipovae	3.2	3.1	1.4 ± 1.1	38.0	*T. filippovae*	3.1	3.2	1.5 ± 1.2	40.7
Architeuthis sp.	2.7	0.3	1.4 ± 0.9	41.4	*T. pellucida*	2.0	0.7	1.3 ± 1.4	43.8
Histioteuthis B4	21.3	12.2	1.3 ± 1.3	44.6	*K. longimana*	1.4	2.7	1.3 ± 1.2	46.9
T. pellucida	2.2	1.6	1.3 ± 1.2	47.7	*H. reversa*	0.6	1.9	1.3 ± 1.0	49.9
K. longimana	0.7	2.3	1.2 ± 1.3	50.8	*O. rugosa*	1.6	1.5	1.3 ± 1.4	52.8

(i) differences in sampling methodology, and (ii) development of tools permitting identification of hard parts to taxa lower than family or genus, and (iii) spatial differences in prey diversitiy. Other dietary studies are often composed of very small sample sizes or involve much smaller subsampling proportions than those in this study. Such sampling regimes may exclude cephalopod species present in very small numbers in diet samples and therefore, underestimate prey species diversity. Species identification of cephalopods has also improved with increased sample sizes of fresh specimens available for species description and improved access to comprehensive archival reference collections. In some oceanic regions,

sperm whales have been observed to feed primarily on specific prey items (e.g. the Humbolt Current (Clarke *et al.*, 1988). Species diversity within diet samples is likely to reflect that of the prey diversity within a given foraging region.

Cephalopod species composition in this study was dominated by members of the same families reported in sperm whales from other areas of the Southern Hemisphere: the Histioteuthidae, Onychoteuthidae, Ommastrephidae, Cranchiidae, and Pholidoteuthidae families (Gaskin and Cawthorn, 1967; Clarke *et al.*, 1976; Clarke, 1980; Clarke *et al.*, 1980; Mikhalev *et al.*, 1981; Clarke and MacLeod, 1982; Clarke *et al.*, 1988; Pascoe *et al.*, 1990; Clarke
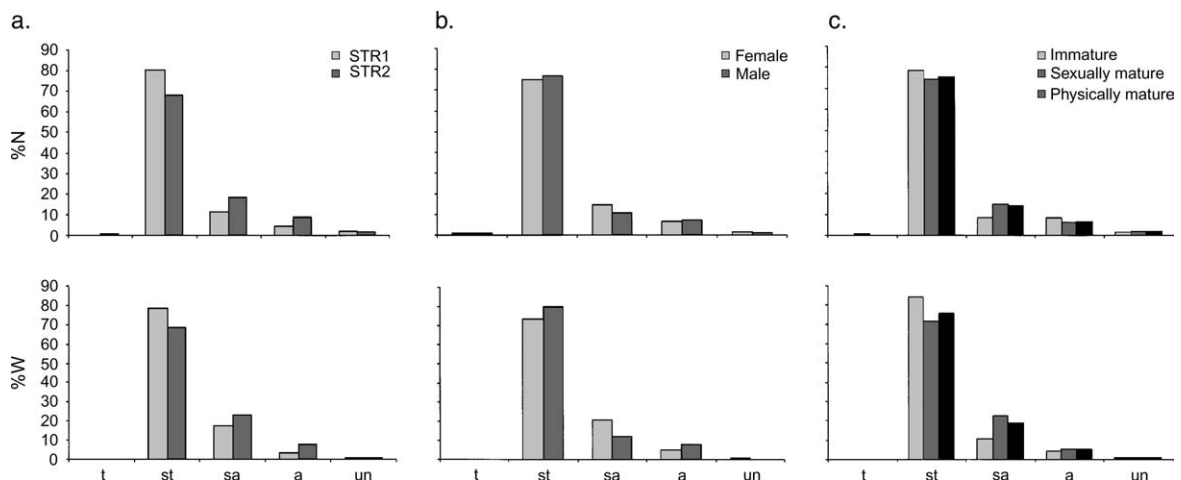

Figure 3. Percentage abundance by number (%N) and by estimated wet weight (%W) of cephalopod species ecotype groups for (a) stranding, (b) sex, and (c) age groups. Ecotype groups: t: tropical; st: subtropical; sa: sub-Antarctic; a: Antarctic; un: unknown.

Table 5. Mean lower rostral lengths, calculated mean mantle lengths and mean estimated wet weight $\pm$ s.d. (range) of cephalopod species in the stomachs of sperm whales from Tasmania (all samples pooled, n = 36).

Species (n)	LRL (mm)	ML (mm)	Wet weight (g)	Species (n)	LRL (mm)	ML (mm)	Wet weight (g)
Haliphron atlanticus (12)	14.6 ± 3.7 (9.6−22.4)	n/a	1 012.9 ± 856.4 (404.7−3 532.0)	*Histioteuthis* sp. Type A (158)	6.1 ± 0.9 (3.8−7.4)	187.5 ± 31.0 (84.4−237.9)	230.0 ± 63.4 (65.3−377.4)
Ancistrocheirus lesueuri (1 043)	7.3 ± 1.2 (3.8−14.4)	259.3 ± 48.0 (113.6−544.9)	1 241.1 ± 1 105.1 (95.5−10 952.6)	*Histioteuthis* B1 (1 259)	5.6 ± 0.7 (3.0−7.5)	110.8 ± 15.1 (53.0−153.0)	191.9 ± 44.9 (53.9−340.0)
Architeuthis sp. (215)	12.0 ± 2.7 (4.7−18.7)	655.7 ± 164.0 (223.2−1 053.5)	21 486.6 ± 23 580.4 (200.2−110 233.1)	*Histioteuthis eltaninae* (1 810)	4.7 ± 0.3 (2.6−6.3)	90.4 ± 7.0 (48.6−126.3)	132.5 ± 17.8 (46.9−239.5)
Japetella sp. (39)	4.7 ± 2.1 (2.5−8.7)	n/a	n/a	*Histioteuthis* B2 (6 186)	5.2 ± 0.7 (2.5−8.0)	101.9 ± 14.8 (41.9−164.1)	165.7 ± 43.7 (37.4−389.0)
Chiroteuthis joubini (316)	7.4 ± 0.7 (3.9−12.8)	192.2 ± 20.7 (106.8−324.5)	184.8 ± 132.2 (16.3−2 208.4)	*Histioteuthis reversa* (345)	4.8 ± 0.5 (3.5−6.1)	93.7 ± 10.3 (64.1−121.9)	141.9 ± 27.5 (73.5−224.5)
Chiroteuthis veryani (1 361)	6.7 ± 0.7 (3.4−8.6)	175.3 ± 17.9 (94.6−221.8)	151.7 ± 149.8 (21.4−2 697.3)	*Histioteuthis atlantica* (4 635)	5.2 ± 0.6 (3.1−7.9)	123.8 ± 16.2 (69.1−192.3)	168.8 ± 43.3 (57.6−401.9)
Chiroteuthis sp. (15)	7.9 ± 1.7 (5.0−9.7)	207.4 ± 39.6 (133.7−248.7)	252.7 ± 117.8 (60.0−465.3)	*Histioteuthis* B4 (7 011)	5.4 ± 0.6 (2.5−7.8)	105.5 ± 14.0 (41.9−159.6)	176.2 ± 41.9 (37.4−389.0)
Chtenopteryx sp.? (1)	1.5 (1.5)	60.3 (60.3)	19.7 (19.7)	*Histioteuthis* sp. Type B (449)	5.6 ± 0.7 (3.5−7.2)	112.2 ± 16.5 (64.1−146.3)	195.3 ± 50.0 (73.5−313.2)
Cranchia scabra (60)	3.4 ± 0.5 (2.1−4.6)	148.4 ± 26.5 (76.6−198.1)	43.8 ± 11.4 (17.9−75.3)	*Lepidoteuthis grimaldii* (2 251)	11.7 ± 2.6 (6.2−23.5)	577.7 ± 123.9 (302.9−1 172.7)	n/a
Galiteuthis glacialis (1 279)	5.7 ± 0.8 (1.3−8.4)	483.8 ± 68.3 (115.7−710.5)	73.2 ± 23.5 (2.7−338.8)	*Idioteuthis cordiformis* (442)	6.5 ± 1.0 (4.0−11.6)	186.5 ± 30.5 (20.6−335.5)	279.6 ± 135.9 (65.1−1 398.1)
Galiteuthis pacifica (5)	4.8 ± 0.9 (3.7−5.9)	408.8 ± 74.2 (316.7−501.0)	49.5 ± 19.5 (26.9−75.2)	*Mastigoteuthis psychrophile* (3)	4.2 ± 0.6 (3.7−4.8)	120.3 ± 3.5 (117.4−124.2)	25.8 ± 6.3 (20.7−32.8)
Megalochranchia sp. (214)	8.4 ± 1.8 (4.3−12.8)	518.0 ± 125.9 (222.1−902.9)	360.3 ± 227.5 (48.1−1 616.7)	*Mastigoteuthis* sp. (25)	4.7 ± 0.8 (3.3−6.5)	135.3 ± 23.0 (64.2−187.2)	112.4 ± 52.9 (37.4−263.7)
Mesonychoteuthis hamiltoni (770)	14.6 ± 5.8 (2.9−40.7)	886.6 ± 359.7 (165.9−2 640.7)	916.9 ± 991.6 (22.6−7 000.0)	*Octopoteuthis rugosa* (709)	10.9 ± 2.2 (6.6−20.5)	187.5 ± 38.2 (23.6−354.9)	313.9 ± 175.0 (92.3−1 389.3)
Taonius pavo (932)	8.8 ± 1.0 (5.4−12.9)	527.1 ± 61.8 (319.4−780.2)	260.1 ± 64.1 (88.2−593.7)	*Taningia danae* (278)	15.6 ± 3.5 (8.8−23.2)	618.4 ± 265.6 (105.0−1 188.2)	6 107.2 ± 4 115.6 (708.9−19 516.2)
Teuthowenia pellucida (822)	7.4 ± 0.8 (3.4−9.6)	244.2 ± 23.8 (123.9−367.0)	228.9 ± 51.1 (36.3−411.8)	*Nototodarus gouldi* (305)	12.1 ± 1.5 (5.2−14.8)	455.3 ± 50.4 (218.6−603.6)	2 911.0 ± 895.4 (250.9−4 997.2)
Cycloteuthis akimushkini (4)	7.5 ± 1.8 (4.8−8.5)	231.7 ± 55.6 (148.8−263.5)	347.9 ± 139.1 (141.0−429.7)	*Ommastrephes bartrami* (49)	12.8 ± 1.4 (7.2−15.2)	498.4 ± 54.0 (287.8−589.6)	2 810.7 ± 681.8 (720.1−4 137.4)
Discoteuthis discus (14)	7.2 ± 0.8 (5.5−8.4)	n/a	n/a	*Todarodes filippovae* (1 085)	11.9 ± 1.4 (4.3−15.8)	446.6 ± 50.8 (188.0−582.8)	2 075.9 ± 669.4 (115.0−4 901.2)
Gonatus antarcticus (59)	6.8 ± 0.6 (5.2−8.2)	250.2 ± 26.2 (179.5−308.1)	320.5 ± 90.7 (125.8−573.5)	*Kondakovia longimana* (518)	10.9 ± 2.8 (5.3−21.2)	419.2 ± 124.4 (169.0−914.9)	1 782.7 ± 2 438.2 (21.5−30 729.1)
Histioteuthis A1 (65)	5.7 ± 0.6 (3.8−7.4)	164.8 ± 21.5 (101.0−221.2)	199.1 ± 44.4 (86.7−331.0)	*Moroteuthis 'A'/ingens* (113)	10.5 ± 1.2 (3.2−12.2)	424.2 ± 51.2 (120.3−497.6)	2 085.9 ± 576.7 (51.6−3 227.4)

Species			
Histioteuthis macrohista (275)	4.7 ± 1.2 (2.4–7.4)	70.8 ± 18.2 (35.2–106.5)	144.8 ± 69.3 (34.4–313.2)
Histioteuthis melaegroteuthis (317)	3.1 ± 0.3 (2.3–4.8)	63.8 ± 12.6 (37.5–94.4)	60.0 ± 11.3 (31.6–138.7)
Histioteuthis bonnellii (2 524)	5.7 ± 0.6 (2.7–7.9)	88.3 ± 8.9 (43.0–122.2)	196.9 ± 39.9 (43.6–412.4)
Histioteuthis celetaria pacifica (16)	6.3 ± 1.1 (3.3–8.9)	176.3 ± 35.0 (84.4–221.2)	259.7 ± 93.8 (65.3–479.6)
Histioteuthis miranda (510)	6.5 ± 0.6 (4.3–8.7)	195.1 ± 20.0 (120.6–271.1)	575.8 ± 127.2 (208.9–1 166.2)
Histioteuthis hoylei (969)	6.1 ± 0.8 (3.6–9.2)	95.7 ± 12.0 (60.1–141.6)	327.8 ± 99.3 (87.1–859.9)
Moroteuthis knipovitchi (314)	4.9 ± 0.6 (3.0–8.0)	149.3 ± 59.3 (−52.5–474.0)	267.7 ± 148.6 (43.7–1 438.3)
Moroteuthis lonnbergii (204)	6.3 ± 0.7 (3.4–7.7)	n/a	615.8 ± 212.4 (67.7–1 183.6)
Moroteuthis robsoni (1 288)	9.2 ± 1.2 (4.5–12.3)	732.3 ± 185.1 (56.9–1 204.8)	8 604.8 ± 6 806.1 (27.5–64 046.9)
Pholidoteuthis adami (14)	4.6 ± 1.1 (2.8–7.2)	198.8 ± 46.6 (126.4–307.2)	225.4 ± 173.5 (48.9–708.2)
Pholidoteuthis boschmai (2 131)	9.8 ± 1.7 (5.4–18.1)	413.2 ± 69.9 (233.2–755.0)	1 823.1 ± 973.0 (313.7–9 618.4)
Vampyroteuthis infernalis (20)	10.7 ± 2.1 (5.5–14.5)	90.3 ± 19.4 (43.8–125.0)	431.3 ± 275.7 (31.3–1 142.6)

and Roeleveld, 1998; Clarke and Roper, 1998). The Histioteuthidae appear to be an important family numerically in the diet of sperm whales in temperate waters globally (Clarke, 1980; Kawakami, 1980; Clarke, 1996; Clarke and Young, 1998).

Size of cephalopods
The maximum calculated mantle lengths in this study were often larger than that reported for cephalopod species in the literature. Cephalopods are difficult to sample using conventional methods. Large individuals often avoid nets and are therefore under-represented in samples (Clarke, 1983). Cephalopod predators are undoubtedly more efficient at catching these larger size classes and therefore, provide a more accurate assessment of cephalopod size structure (Clarke, 1983). Lower rostral lengths of cephalopods ranged over similar sizes or encompassed that found in the diet of sperm whales in other regions (Clarke and Macleod, 1974; Clarke and Macleod, 1976; Clarke, 1980; Fiscus *et al.*, 1989; Smith, 1992; Clarke and Young, 1998; Smith and Whitehead, 2000).

Although cephalopods less than 300 mm DML dominated the diet, larger species actually contributed far more in terms of biomass to the diet of these animals, with those larger than 1000 g in estimated wet weight comprising 78.6% of the total estimated wet mass. The irregular consumption of larger species appears to be an important, efficient source of energy for an animal that is estimated to consume between 3% and 4% of its own body mass per day (Lockyer, 1981). If the average weight of prey consumed is 233.7 g and the average weight of the sperm whales in this study is 12.3 tonnes ($W_t = 0.006648 L_m^{3.18}$; Lockyer, 1981), the estimated number of prey items eaten by an individual (calculated as the mean of 3−4%) would equate to 1842.1 individuals per day. This clearly highlights the importance of larger species in efficiently acquiring energy, thereby reducing the number of prey items required to meet energetic demands.

Cephalopod species composition and size with respect to stranding site, sex, and age
While significant differences were found in the species composition of the diet of individuals on the basis of stranding site and sex and in the size of prey items on the basis of stranding site and age, high individual variability was observed within all groups. This may be the result of two factors: (a) the social structure of sperm whale groups and/or (b) individual foraging behaviour. The social structure of female sperm whale groups is such that each group is based on a dynamic association of a number of smaller units. These smaller units comprise long-term associations between 12 to 13 individuals that may or may not be related to each other (Whitehead *et al.*, 1991; Whitehead and Kahn, 1992; Mesnick *et al.*, 2003). Preliminary genetic analyses demonstrate the presence of both related and unrelated individuals within the stranding
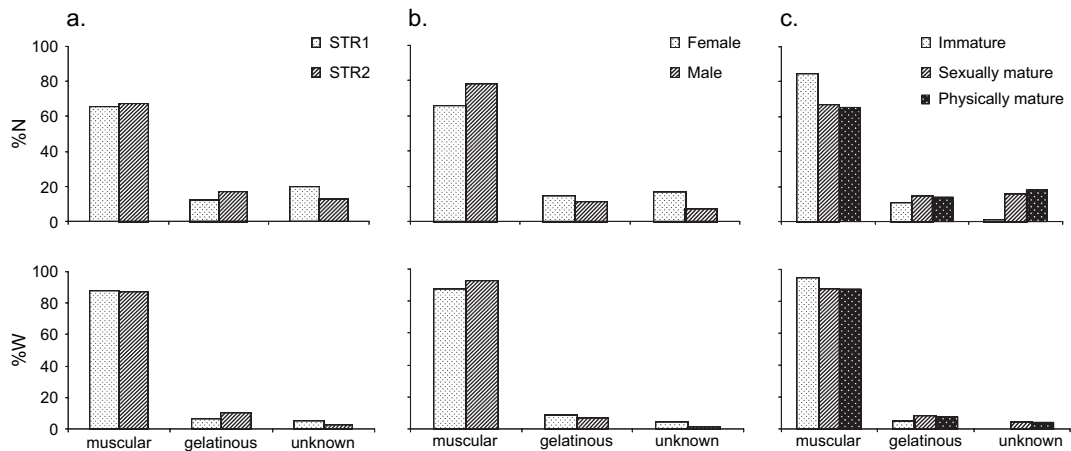
Figure 4. Percentage abundance by number (%N) and by estimated wet weight (%W) of muscular and gelatinous cephalopod species for (a) stranding, (b) sex, and (c) age groups.

groups (Mesnick, 2001; Mesnick *et al.*, 2003). It is probable that these two stranding groups (STR1: n = 66; STR2: n = 35) are composed of several of these dynamic associations and that therefore, differences between stranding sites are more reflective of differences in the diet of individuals within these smaller units. Moreover, sperm whales observed in the field while associating with others in their group at the surface, separate three-dimensionally on diving (Watkins and Schevill, 1977). Separation of foraging individuals is advantageous as it prevents animals from searching through low prey density areas recently encountered by other whales. This separation of foraging individuals would be expected to result in at least some degree of individual variation in prey items encountered and therefore, overall diet.

Differences in the species composition of the diet of males and females may be reflective of different foraging habitats between sexes. The ages of males in this study ranged between 5 and 24 yr, the majority of which (5 of 6) were between 19 and 24 yr and involved in STR2. Dispersal of males from their natal group is reported to occur at 6−10 yr (Best, 1979; Richard *et al.*, 1996) or 15 yr (Rice, 1989). However, on leaving their natal groups males associate with others of a similar size rather than age group,

with groups observed to contain 12−15 individuals (or multiples thereof) 10−29 years old (Best, 1979). It is possible that the males in this study (excluding the 5-yr-old, which is likely to have been associated with its maternal unit) were part of a bachelor group of males foraging in a similar area, but separate to the female groups in this study and had joined the female groups just prior to the strandings.

The diet of individuals in age groups 2 and 3 did not appear to reflect a predominance of either large or small
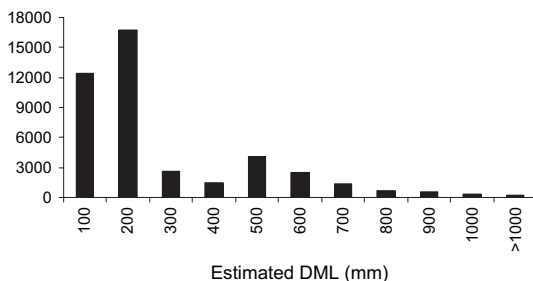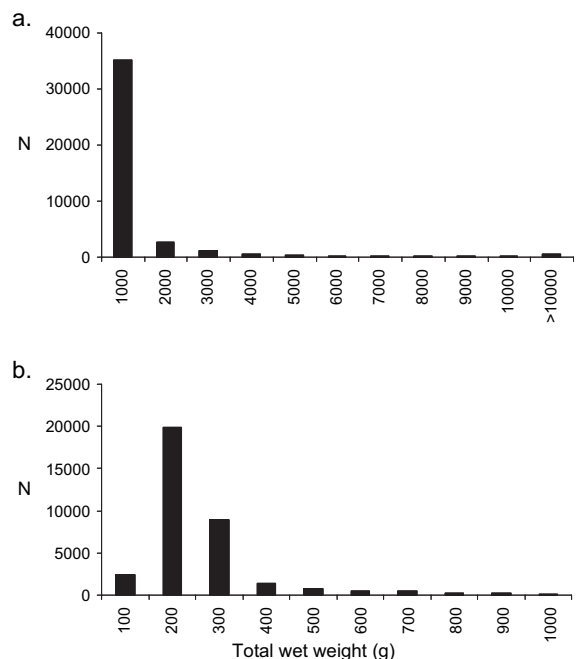

Figure 6. Distribution of the estimated wet weights of cephalopod prey in the diet of southern Australian sperm whales: (a) all estimated wet weights; (b) estimated wet weights less than 1000 g only.

Figure 5. Distribution of the dorsal mantle lengths of cephalopod prey in the diet of southern Australian sperm whales.

Table 6. Cephalopod species for which LRLs differed significantly between stranding site and age groups.

	Site (d.f. = 2)			Age (d.f. = 1)	
Species	f-ratio	p	Species	f-ratio	p
Architeuthis sp.	4.3	0.02	*C. scabra*	6.4	0.02
C. v. veryanii	5.9	0.003	*G. glacialis*	14.3	0.0002
H. macrohista	76.0	0.0001	*H. macrohista*	18.4	0.0001
H. bonnellii	9.1	0.003	*H. bonnellii*	9.1	0.003
Histioteuthis sp. A(1)	13.8	0.0001	*H. hoylei*	9.1	0.003
Histioteuthis B1	8.1	0.0003	*Histioteuthis* sp. A(1)	5.6	0.02
Histioteuthis B2	312.7	0.0001	*Histioteuthis* B1	44.3	0.0001
H. atlantica	32.4	0.0001	*Histioteuthis* B4	14.8	0.0001
Histioteuthis B4	9.0	0.0001	*Histioteuthis* sp. B(1)	4.3	0.04
Histioteuthis sp. B(2)	8.6	0.0003	*Histioteuthis* sp. B(2)	12.1	0.001
I. cordiformis	15.9	0.0001	*K. longimana*	8.4	0.004
L. grimaldii	75.3	0.0001	*L. grimaldii*	30.4	0.0001
M. hamiltoni	4.4	0.01	*M. ingens*	3.9	0.05
M. lonnbergii	14.4	0.0001	*M. lonnbergii*	14.7	0.0002
M. robsoni	8.6	0.0002	*M. robsoni*	40.2	0.0001
N. gouldi	14.4	0.0001	*T. pellucida*	6.5	0.01
O. rugosa	33.5	0.0001			
P. boschmai	8.0	0.0004			
T. pavo	5.3	0.005			
T. filippovae	36.6	0.0001			

cephalopod species. Differences in the size of prey consumed between individuals in these age groups are likely to be influenced by the high variability observed in the diet of individuals and possible separation of foraging habitats between sexes (all males were in age group 2).

Cephalopod species ecotype and tissue composition
The high species diversity of cephalopods observed in the diet of individuals in this study and the wide range of ecotypes these species are recorded from suggest that large scale movements are undertaken by female groups of sperm whales. Female sperm whales range large distances of at least 600×600 nautical miles from equatorial waters to around 40°S (Rice, 1989; Jaquet *et al.*, 2000). Marking programmes around Australia have reported sperm whales of both sexes moving between the eastern Indian Ocean and southwest Pacific, across southern Australia and also between eastern Australia and New Zealand (Brown, 1981). Movements of sperm whales in search of food are thought to be in the order of 55 nautical miles per day (Jaquet *et al.*, 2000), however daily displacement of individuals varies with foraging success (Jaquet and Whitehead, 1999; Rendell *et al.*, 2004).

The presence of cephalopod species from tropical to Antarctic regions therefore also represents movements over considerable temporal scales. There are few data on the passage rates and retention of the hard part remains of cephalopods. Clarke (1980) reported that an average female sperm whale would retain cephalopod beaks for 2.1 to 2.5 days while males would retain beaks for 1.2 to 1.6 days.

Captive bottlenose dolphins (*Tursiops truncatus*) retain cephalopod beaks for up to three days (Ross, 1979). The presence of cephalopod species described from tropical and Antarctic regions in the diet of individual sperm whales suggests that cephalopod beaks may be retained for longer periods than previously thought.

The numerical abundance and percentage wet weight of species on the basis of ecotypes varied between stranding sites, sexes, and age groups. However, all groups demonstrated a diet dominated by subtropical prey species. Those differences observed are likely to be the result of high individual variability in prey items encountered rather than a distinct separation of foraging habitat between individuals in each group and may also reflect individual variation in digestions and hard part retention.

The presence of the Antarctic species *G. glacialis*, *Gonatus antarcticus*, *K. longimana*, *Mastigoteuthis psycrophila*, and *Moroteuthis knipovitchi* in the diet of female and immature sperm whales may be the result of (i) the redistribution of prey species northwards as a result of oceanographic conditions or (ii) movement of female groups of sperm whales further south than are generally considered to occur. A number of sub-Antarctic and Antarctic species of cephalopods have been recorded north of their usual range in association with northwardly moving cold water currents (Nesis, 1972; Imber, 1978; Alexeyev, 1994). Often frontal systems such as the subtropical and sub-Antarctic convergences serve as boundaries to the distribution of cephalopod species (Clarke, 1980; Voss, 1985; Rodhouse *et al.*, 1992; Dunning, 1993). Rather than

being stable, non-moving boundaries, these are dynamic, moving their geographic position continuously depending on both broad-scale and localized oceanographic conditions. Consequently, species associated with these boundaries also redefine their distributions. Frontal system movements may have redistributed these Antarctic species into those areas utilized by female sperm whales. Clarke and MacLeod (1982) also reported *K. longimana* from female sperm whales caught in the Tasman Sea and suggested that the distribution of this species could be further north than previously thought. They additionally suggested that female sperm whales may range further south than previously reported. Female sperm whales around the New Zealand region have been reported to occur regularly in waters down to 50°S (Gaskin, 1973). This may also occur in the southeast Australian region. Investigations into the movements of female sperm whales and cephalopod species in this region would provide greater insights into possible reasons for the presence of such species in the diet of female sperm whales.

The diet of sperm whales observed in this study was predominantly composed of muscular cephalopods. While a comprehensive assessment on the calorific content of cephalopod species is lacking, those assessments that have been undertaken demonstrate cephalopods to be an appreciably lower source of energy to top predators than fish or crustaceans (Croxall and Prince, 1982). This provides some source of questions as to why a large predator such as the sperm whale, which needs to consume 3−4% of its body mass per day (Lockyer, 1981), would concentrate it's efforts on such a prey group. A foraging strategy involving the utilisation of a readily available, highly abundant food source that can be found in large aggregations may serve as a more efficient means of meeting energetic requirements rather than one involving potentially long and energetically expensive search times for higher quality prey items. Further, the presence of muscle tissues is likely to be of importance to a predator providing a relatively higher source of protein than other non-muscular species within this relatively energy de-pauperate food group.

The cephalopod species represented in the diet of the sperm whales in this study are reported to range throughout the water column to at least depths of 3000 m [Table 3; note that knowledge of the depth at which cephalopods range is largely based on a small number of studies in which only immature or young specimens of those species known to contribute to the diet of sperm whales have been caught. Generally most cephalopod species display ontogenic migration to deeper waters and it is likely therefore, that larger and older members of cephalopods species range to deeper depths (M. R. Clarke, pers. comm.)]. All species, with the exception of *V. infernalis*, occur in waters shallower than 500 m, suggesting that at least the sperm whales in this study may spend a large amount of time foraging in depths of less than 500 m. Published dive data

for sperm whales to date is sparse due to inherent technical and logistical difficulties associated with tracking individuals. Those data that have been published describe diving by females to range between approximately 200 and 1200 m (Lockyer, 1977; Gordon, 1987; Amano and Yoshioka, 2003) and males between approximately 300 and 2000 m (Lockyer, 1977; Watkins et al., 1993). It is likely that individuals spend the majority of their time diving between 500 and 800 m (Watkins et al., 1993; Amano and Yoshioka, 2003). Further advances in tagging technology are likely to provide more substantial insights into the foraging behaviour of sperm whales and in association with this, the distribution of cephalopod prey.

The diet of sperm whales in relation to fisheries in this region

The commercial harvest of cephalopods in this area has been in operation periodically since 1972, targeting the ommastrephids *Nototodarus gouldi*, *T. filippovae*, and *Ommastrephes bartrami* and the sepioteuthid *Sepioteuthis australis*. Fishery effort has varied temporally, with foreign fishing vessels taking up to 7914 tonnes during the 1970s, and domestic catches much lower increasing from 439 to 1673 tonnes between 1995/1996 and 1997/1998 (AFMA, 2001). While *S. australis* was not observed in the samples that composed this study, all the Ommastrephids targeted by the fishery were, comprising 3.9% of the diet numerically and 9.6% by weight. If it is assumed that sperm whales consume 3.5% of their total mass per day (Lockyer, 1981), then after calculating total weight ($W_t = 0.006648L_m^{3.18}$; Lockyer, 1981) of all individuals involved in the Tasmanian strandings (see Evans et al., 2002), the total mass of ommastrephids consumed by this subsample of the total population in southern Australian waters is in the order of 40.1 tonnes. Given that the samples studied here represent only a few days to at most a few weeks of prey consumed, the amount of these commercial species consumed by sperm whales far exceeds that of the current fishery operations in the area. Further information on the diet of sperm whales during other times of the year coupled with information on the distribution and population numbers throughout this region is important in order to understand any potential competition, the distribution of this competition temporally and spatially and the impacts of such competition on both sperm whale and cephalopod populations in this area.

Acknowledgements

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